Multi-scale drivers of microbial biodiversity across small water bodies in northern regions

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Abstract

The patterns and drivers of microbial biodiversity remain less described and understood than those of larger organisms. Considerable knowledge gaps regarding microorganisms remain especially among small water bodies, which contribute significantly to biodiversity across northern landscapes. The main aims of this thesis were (1) to investigate microbial biodiversity patterns and multi-scale drivers along elevational gradients in subarctic streams and ponds; (2) to explore the effects of species niche characteristics and traits on elevational distributions of pond diatoms; (3) to test for the theory of island biogeography and to identify the factors affecting diatom biodiversity in boreal springs; and (4) to investigate the factors shaping diatom biodiversity along a land-use intensity gradient across boreal streams.

To achieve these aims, small streams, ponds, and springs in the boreal and subarctic regions were sampled for microorganisms, and a variety of explanatory variables representing local environmental conditions, catchment properties and climatic and spatial factors were measured or derived from existing databases. The studied microbial groups comprised diatoms, cyanobacteria, and non-cyanobacteria (i.e., bacteria other than cyanobacteria). To examine the relationships between microbial biodiversity and explanatory variables, advanced statistical methods were used.

The results showed that in the subarctic streams, diatom species richness or range size exhibited no consistent elevational patterns, whereas community similarity decreased primarily with elevational distance. Diatom communities among the streams were shaped by local-scale variables, such as water depth, and regional drivers, including dispersal and geographical factors. In the subarctic ponds, the richness–elevation relationship was unimodal for diatoms and cyanobacteria, whereas non-cyanobacteria richness declined with increasing elevation. Ponds at both ends of the elevational gradient harboured taxonomically unique microbial communities. The observed patterns were driven by hierarchically structured factors. The variation in species richness and uniqueness of diatom and cyanobacteria communities were best explained by local-scale variables, whereas non-cyanobacteria were also influenced by terrestrial productivity and elevation. Pond diatom distributions were also affected by species niche characteristics and traits: small size and strong acid tolerance were associated with a wider elevational distribution. At the community level, acidic ponds harboured functionally clustered communities. For spring diatoms, no species–area or species–isolation relationships were found; instead, local environmental variables and catchment characteristics were most strongly associated with species richness and community composition. At the relatively small spatial scale studied, diatom biodiversity was apparently not constrained by dispersal-related factors. Along the land-use intensity gradient, changes in stream diatom communities were evident. More intensive land use resulted in decreasing species richness and com-

munity compositions comprising more pollution-tolerant species. The variation in diatom richness and community composition was influenced by multiple local-scale factors, which in turn were controlled by catchment properties.

In conclusion, this thesis expands current knowledge of microbial biodiversity across small water bodies in the northern regions. Microbial biodiversity in such systems is shaped by multiple factors prevailing at hierarchical spatial scales, the relative importance of which depends on the study system and microbial group. The effects of local-scale factors were emphasised throughout, yet catchment characteristics and spatial variables may also be important. For a deeper understanding of the factors underlying microbial biodiversity, considering multiple inherently different ecosystem types and organism groups is essential.

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I am thankful to my supervisor Prof. Janne Soininen for introducing me to the intriguing world of aquatic microbial biodiversity and freshwater diatoms in particular. I wish to thank him for providing me the opportunity to begin this project and for advice during this work. I also wish to thank my preliminary examiners, Docent Silke Langenheder and Prof. Koen Sabbe, for their encouraging and helpful comments. I am grateful to all the co-authors of the papers for collaboration; without their valuable contributions, the scope of this work would have been much narrower.

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In Helsinki, February 28th 2019

Anette Teittinen

Contents

List of original publications

This thesis is based on the following publications:

I **Teittinen, A.**, Kallajoki, L., Meier, S., Stigzelius, T., Soininen, J. 2016. The roles of elevation and local environmental factors as drivers of diatom diversity in subarctic streams. *Freshwater Biology* 61, 1509–1521.

II **Teittinen, A.**, Wang, J., Strömgård, S., Soininen, J. 2017. Local and geographical factors jointly drive elevational patterns in three microbial groups across subarctic ponds. *Global Ecology and Biogeography* 26, 973–982.

III **Teittinen, A.**, Weckström, J., Soininen, J. 2018. Cell size and acid tolerance constrain pond diatom distributions in the subarctic. *Freshwater Biology* 63, 1569–1578.

IV **Teittinen, A.**, Soininen, J. 2015. Testing the theory of island biogeography for microorganisms — patterns for spring diatoms. *Aquatic Microbial Ecology* 75, 239–250.

V **Teittinen, A.**, Taka, M., Ruth, O., Soininen, J. 2015. Variation in stream diatom communities in relation to water quality and catchment variables in a boreal, urbanized region. *Science of the Total Environment* 530–531, 279–289.*

The publications are referred to in the text by their roman numerals.

* This publication has been previously used in: Taka, M. 2017. Key drivers of stream water quality along an urban-rural transition – a watershed-scale perspective. *Department of Geosciences and Geography* A48.

Authors' contributions to the publications

	Paper **I**	Paper **II**	Paper **III**	Paper **IV**	Paper **V**
Original idea and study design	JS, AT	JS, AT, JWa	AT, JS	JS, AT	MT, JS
Field and laboratory work	LK, SM, TS, JS	AT, JWa, SS, JS	AT, JWe, JS	AT, JS	MT, AT, OR
Data analysis	AT	AT, SS	AT	AT	AT, MT
Manuscript preparation	AT, LK, SM, TS, JS	AT, JWa, SS, JS	AT, JWe, JS	AT, JS	AT, MT, OR, JS
Overall responsibility	AT	AT	AT	AT	AT

AT = Anette Teittinen[a], JS = Janne Soininen[a], JWa = Jianjun Wang[b], JWe = Jan Weckström[c], LK = Liisa Kallajoki[a], MT = Maija Taka[d], OR = Olli Ruth[a], SM = Sandra Meier[e], SS = Simon Strömgård[a], TS = Tiina Stigzelius[a]. [a]) Department of Geosciences and Geography, University of Helsinki, Finland; [b]) State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, China; [c]) Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences and Helsinki Institute of Sustainability Science (HELSUS), University of Helsinki, Finland; [d]) Department of Built Environment, Aalto University, Finland; [e]) Aqua-Ecology GmbH & Co. KG, Germany.

Abbreviations

AIC	Akaike's information criterion
ANOSIM	Analysis of similarities
BRT	Boosted regression trees
DEM	Digital elevation model
FDis	Functional dispersion index
GLM	Generalized linear model
HP	Hierarchical partitioning
LCBD	Local contribution to beta diversity
LM	Linear regression model
m a.s.l.	Meters above sea level
NDVI	Normalized difference vegetation index
OMI	Outlying mean index analysis
OTU	Operational taxonomic unit
RDA	Redundancy analysis
SAR	Species–area relationship
SEM	Structural equation model
TN	Total nitrogen
TP	Total phosphorus
TSS	Total suspended solids
VP	Variation partitioning

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1 Introduction

The diversity of life on Earth is shaped by multiple factors and varies along geographical gradients, such as area, isolation, elevation, and latitude (Lomolino *et al*., 2010). Understanding the causes and consequences of such variation has remained of the key aims for biogeographers and ecologists for a long time, and numerous explanations and hypotheses for biodiversity patterns has been borne out of research on larger organisms (Gaston, 2000; Ricklefs, 2004). For microscopic organisms, such patterns and underlying drivers remain less described and understood. Microorganisms constitute the most diverse and abundant group of organisms, with crucial roles in ecosystem functioning and Earth's biogeochemical cycles (Falkowski *et al*., 2008). Increased knowledge of the factors driving microbial biodiversity is, thus, essential not only for determining whether general biodiversity patterns exist, but also for predicting biodiversity changes and for conserving and restoring ecosystems during the era of accelerating global change (Wang *et al*., 2016; Davison *et al*., 2018).

1.1 Biodiversity patterns and drivers – insights from mountains and islands

Biodiversity is affected by various factors prevailing at multiple spatiotemporal scales (Ricklefs, 1987, 2004; Levin, 1992; Zobel, 1997). Ultimately, the diversity of local biological communities can be viewed as an outcome of regional processes adding species to communities, counteracted by processes able to promote local extinction (Ricklefs, 1987). (1) Large-scale climatic, historical, and evolutionary processes primarily define the regional species pool from which local communities are assembled (Hillebrand and Blenckner, 2002). (2) Dispersal-related factors and (3) abiotic conditions and biotic interactions operating at smaller spatial scales further define the species occurring at a local site (Poff, 1997; Hillebrand and Blenckner, 2002).

To study spatial variation in biodiversity and its underlying mechanisms, elevational gradients on mountains provide ideal natural systems because they cover long environmental and climatic gradients at relatively small spatial extents (Brown, 2001; Sanders and Rahbek, 2012). Exploring elevational biodiversity gradients dates back to the roots of biogeography and has been fundamental to the development of a variety of theories of biodiversity (Lomolino, 2001). Elevational gradients are also useful for predicting the effects of climatic changes on biodiversity (Lomolino, 2001; Rahbek, 2005; Sundqvist *et al*., 2013). Studies have documented that for a variety of taxonomic groups of larger organisms, elevational trends in diversity generally show either unimodal or monotonically decreasing patterns (Figure 1a) (Rahbek, 2005). To explain such elevational patterns, several hypotheses have been proposed (Grytnes and McCain, 2007 and references therein). Some of them emphasise the effects of climatic and local abiotic factors, such as temperature, precipitation, disturbance regimes, or biotic processes, such as ecotone effects and source–sink dynamics. Others, in turn, highlight the role of historical processes, including extinction, speciation and dispersal, or spatial factors, such as area or geometrical boundaries, such as mid-domain effect. The mid-domain effect (reviewed in Colwell *et al*., 2004) predicts that diversity peaks at mid-elevations because randomly distributed species ranges overlap more towards the middle of the elevational gradient as opposed to the mountain base and summit. Additionally, Rapoport's elevational rule (Stevens, 1992) has been used to explain species distributions along elevational gra-

dients. Rapoport's elevational rule is equivalent to Rapoport's latitudinal rule (Stevens, 1989), and hypothesises that because climatic variability increases towards higher elevations, species inhabiting high elevations must tolerate large climatic variation, and consequently have broader elevational ranges compared to species occurring at lower elevations.

Although elevational gradients for macroorganisms are well established, no consensus over the generality in the patterns has been reached for microorganisms (Wang *et al*., 2017) as highly contrasting trends, such as decreasing (Ormerod *et al*., 1994; Bryant *et al*., 2008; Wang *et al*., 2011), increasing (Wang *et al*., 2011), and unimodal (Singh *et al*., 2012) patterns or no significant trends (Jüttner *et al*., 2010; Fierer *et al*., 2011) have been found for different microbial groups. Moreover, different microbial groups may show contrasting biodiversity patterns even within the same study system. For example, Wang *et al*. (2012) demonstrated a significant elevational distance decay for diatoms, but not for bacteria, along a stream elevational gradient. This outcome presumably indicated that dispersal ability and adaptability regarding environmental conditions differ between the two taxonomic groups.

In addition to mountainous regions, research on insular systems has greatly contributed to the understanding of processes shaping biodiversity. In their theory of island biogeography, MacArthur and Wilson (1967) proposed that insular species richness is determined by the size and isolation of an ecosystem. These island characteristics regulate species immigration and extinction rates, such that the number of species increases with the area of an island and decreases with its isolation from potential immigration sources (Figure 1b). The species–area relationship (SAR) had a foundational role in the development of the theory. The SAR depicts the relationship between sampling area and the species richness within the area, and it is considered as one of the most universal species richness patterns for macroorganisms (Arrhenius, 1921; Gleason, 1922; Rosenzweig, 1995). The extent to which microorganisms conform to this pattern remains contested, however, as positive (Horner-Devine *et al*., 2004; Smith *et al*., 2005), non-significant (Soininen and Luoto, 2012) and negative SARs (Logue *et al*., 2012) have been reported. The relationship between species richness and isolation among macroorganisms is not as general as the SAR (Whittaker and Fernández-Palacios, 2007); for microbes, some studies find support for the

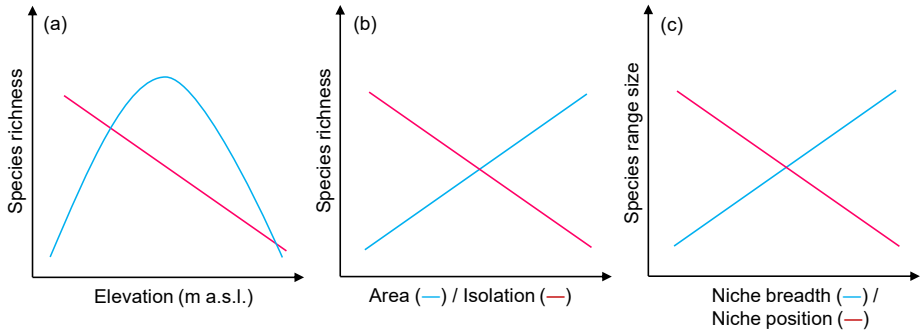

Figure 1. Trends in biodiversity often observed among larger organisms. (a) Species richness typically exhibits a unimodal or a decreasing elevational pattern. (b) According to the theory of island biogeography (MacArthur and Wilson, 1967), species richness increases with island area and decreases with its isolation from potential sources of immigration. (c) A niche breadth hypothesis proposes that species geographical distribution and niche breadth are positively correlated (Brown, 1984); a niche position hypothesis invokes that species using more widespread habitats and resources (Hanski *et al*., 1993) have broader distributions than species preferring less typical environments.

pattern (Vyverman *et al*., 2007; Benito *et al*., 2018), while others do not (Reche *et al*., 2005).

Species geographical distributions can also be viewed as a spatial reflection of their niche characteristics (Gaston, 2003; Lomolino *et al*., 2010). According to a niche breadth hypothesis, species that have a broad tolerance towards environmental conditions become more widely distributed (Brown, 1984), such that there would be a positive relationship between species geographical distribution and niche breadth (Figure 1c). A recent meta-analysis proposed that the relationship could be a general ecological pattern (Slatyer *et al*., 2013). Gaston and Blackburn (2000) invoked instead that niche position, an indicator of habitat and resource availability (Hanski *et al*., 1993), can be more important than niche breadth in determining species distributions (Figure 1c). Niche position is typically used to measure whether the environmental conditions where a species occurs are common across the study region. The reasoning behind this hypothesis is that species that can utilise widely distributed habitats and resources are more widespread compared to species preferring less typical environments. Evidence complementing this hypothesis exists for both macro- (Gregory and Gaston, 2000; Heino and Grönroos, 2014; Rocha *et al*., 2018) and microorganisms (Heino and Soininen, 2006; Rocha *et al*., 2018).

1.2 Small water bodies

Small water bodies constitute the most numerous freshwater habitats globally, are vital for freshwater biodiversity and play an important role in providing ecosystem services (Biggs *et al*., 2017). The term "small water bodies" has no univocal, universally accepted definition. In this thesis, the term is used to refer to small streams, ponds, and springs. While small size characterises all such ecosystems, other properties vary greatly among different types of small water bodies. Small water bodies often represent the least degraded freshwater habitats, serving refuges for sensitive and rare species (Cantonati *et al*., 2012a; Biggs *et al*., 2017). They are threatened, however, by a number of stressors, including land-use changes, degradation of habitats and water quality, and climate change (Heino *et al*., 2005; Jyväsjärvi *et al*., 2015; Biggs *et al*., 2017). Despite their importance, small water bodies are understudied and considerable knowledge gaps regarding their biodiversity remain; for instance, even basic surveys are lacking for many groups of microorganisms (Biggs *et al*., 2017). Expanding current knowledge of microbial biodiversity in small water bodies is hence of utmost importance.

Streams are naturally hierarchical and heterogeneous systems, characterised by unidirectional flow (Frissell, 1986). Their spatial and temporal heterogeneity is high and often more dynamic than in standing waters (Wetzel, 2001). Streams are highly connected systems with longitudinal changes in flow, water chemistry, and biota. In contrast to standing freshwaters, running freshwater ecosystems are prone to disturbances induced by flow fluctuations, such as desiccation and flood disturbance, which can affect their structure and function (Peterson and Stevenson, 1992; Biggs and Smith, 2002; Biggs *et al*., 2005).

Ponds are small standing freshwater ecosystems that are typically distinguished from lakes by their smaller size (Biggs *et al*., 2017). In this thesis, small standing waters typically smaller than one hectare in area are considered ponds. Although the discrimination between lakes and ponds is somewhat arbitrary, they do differ in many aspects important for aquatic biota. For example, ponds do not typically establish a thermal stratification and they are sufficiently shallow such that light reaches the bottom, enabling primary production in the benthos (Wetzel, 2001). In shallow water bodies, the littoral often stretch-

es over the whole basin, and its structure and productivity dominate the ecosystem. At high latitudes, ponds typically freeze solid during the winter, preventing the occurrence of fish (Rautio *et al*., 2011).

Springs differ from other aquatic systems because they are dependent on continuous flux of groundwater. Non-thermal springs are places where groundwater emerges to the Earth's surface, creating a spring ecosystem. Springs form multidimensional ecotones connecting terrestrial and aquatic ecosystems, and surface and ground waters (Cantonati *et al*., 2012a). Because springs are fed by groundwater, they typically exhibit relatively little variation in thermal and discharge regime, providing unique, relatively stable aquatic habitats (van der Kamp, 1995). They typically have high habitat heterogeneity and contribute greatly to local and regional biodiversity (Ilmonen and Paasivirta, 2005; Cantonati *et al*., 2012a). In isolated aquatic systems within a terrestrial landscape, such as springs and ponds, geographical and physicochemical barriers separate habitats suitable for aquatic organisms; thereby, their biota may be more dispersal limited owing to the lower degree of connectivity between habitats (Soininen, 2007; Cantonati *et al*., 2012a; De Bie *et al*., 2012).

1.3 Diatoms and bacteria in benthic environments

In aquatic ecosystems, diverse microbiota typically grows on and attached to surfaces submerged in the water. This assemblage of microbial organisms, including algae, bacteria, and fungi, embedded in an extracellular matrix on a variety of submerged surfaces (e.g., rocks, sediment, sand, and plants) is called biofilm (Allan and Castillo, 2007). In many aquatic environments, most microorganisms live within biofilms, which are essential sites for carbon and nutrient cycling as well as primary production (Costerton *et al.*, 1995; Vadeboncoeur *et al*., 2003). Benthic assemblages may dominate primary production especially in small and shallow, oligotrophic water bodies where light reaches the bottom (Vadeboncoeur *et al*., 2003).

A diverse group of microscopic algae widely distributed in almost all aquatic environments, are the diatoms (Bacillariophyceae) (Round *et al.*, 1990). Diatoms significantly contribute to primary production and play vital roles in food webs of many aquatic ecosystems. Individual diatoms are encapsulated within siliceous cell walls, forming a shell called the frustule (Round *et al*., 1990). Diatoms are essentially unicellular, yet they exhibit several life-forms as adaptations to, for example, attachment, nutrient capture, and light (Round *et al*., 1990; Rimet and Bouchez, 2012). Information on the capacity of species to utilise nutrient resources and endure physical disturbance (Passy, 2007a) or chemical stress (Soininen *et al*., 2016) can subsequently be used to classify the life-forms into ecological guilds. Besides varying in growth morphology, diatoms exhibit notable interspecific differences in cell size (Krammer and Lange-Bertalot, 1986, 1988, 1991a,b). Cell size is often negatively associated with species distribution as small species tend to be more widespread than large species (Passy, 2012). Diatoms possess many characteristics that make them excellent indicators of both present and past environmental conditions. For instance, many species have relatively narrow tolerances towards several environmental factors, community composition changes relatively rapidly in response to changing environmental conditions, and, because of their siliceous cell walls, diatoms typically preserve well in sedimentary deposits (Smol and Stoermer, 2010).

In addition to diatoms, another important component of benthic assemblages are cyanobacteria, which are photosynthetic prokaryotes

that differ from other bacteria particularly for their photosynthetic mechanism and oxygen production (Vincent, 2009). They are common in many aquatic environments, where they have important roles in nitrogen, carbon, and oxygen dynamics. In high-latitude freshwaters, cyanobacteria are typically highly successful, especially in the benthic environment, and may dominate total biomass and primary productivity (Vincent and Quesada, 2012).

In general, bacteria are considered the most successful forms of life on Earth, regarding total biomass and the variety of habitats colonised (Costerton *et al*., 1995). Within aquatic systems, bacteria present major decomposers and bacterial activity has fundamental effects on nutrient cycling and energy fluxes (Wetzel, 2001). The metabolic transformation of both autochthonous and allochthonous organic matter by bacteria (and fungi) is crucial for the functioning of aquatic ecosystems. A large fraction of the organic matter is decomposed in the benthic environment (Wetzel, 2001).

1.4 Factors affecting microbial biodiversity

Biodiversity of larger organisms is shaped by factors prevailing at multiple spatiotemporal scales (Rosenzweig, 1995; Lomolino *et al*., 2010), yet their importance in influencing microbial biodiversity has been contested during the recent years. Microorganisms have been suggested to be cosmopolitans because of their large population sizes facilitating ubiquitous dispersal (Finlay, 2002) and diminishing the threat of local extinctions (Fenchel and Finlay, 2004). Accordingly, microbial communities should not be constrained by dispersal barriers or historical processes but controlled primarily by contemporary environmental factors, a hypothesis encapsulated by Baas Becking (1934) as ”everything is everywhere, but, the environment selects”.

In contrast to this view, several lines of recent evidence show that microorganisms do exhibit biogeographical patterns that cannot be explained by current local environmental conditions alone (Martiny *et al*., 2006; Fierer, 2008; Hanson *et al*., 2012). During the last decade, research on microbial biogeography has increased considerably (Figure 2), and microbial communities are now generally considered to be controlled not only by current ecological drivers, but also constrained by dispersal-related, historical, and evolutionary processes (Telford *et al*., 2006; Langenheder and Ragnarsson, 2007; Vyverman *et al*., 2007; Verleyen *et al*., 2009; Soininen *et al*., 2016). The relative importance of the factors shaping microbial biodiversity has been suggested to be scale-dependent, such that environmental effects should be more important at small spatial scales, whereas at large geographical extents, spatial and dispersal-related factors may override environmental effects (Martiny *et al*., 2006, Soininen, 2007). However, spatial factors and historical events have been shown to influence microbial communities also at very small scales, such as less than 500 m (Langenheder and Ragnarsson, 2007). In contrast, local environmental factors have been shown to drive microbial communities even at large spatial scales (Van der Gucht

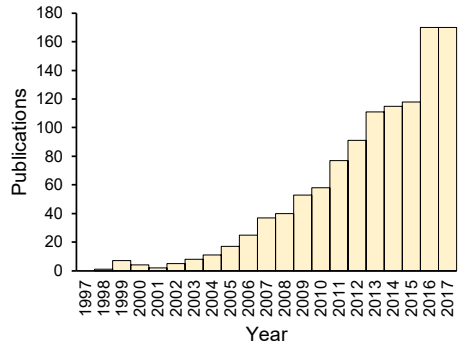

Figure 2. Yearly publications on microbial biogeography in 1997–2017. The data were gathered by searching the Web of Science using a combination of keywords “microbial” and “biogeography”.

et al., 2007; Souffreau *et al*., 2015).

In freshwater ecosystems, the ecological factors affecting microbial communities at a local scale comprise abiotic variables, such as water chemistry, water temperature, light intensity, substrate, and current velocity, and biotic factors, such as competition and grazing (Biggs *et al*., 1990; Stevenson *et al*., 1996; Stevenson, 1997). Factors operating at regional spatial scales, including land use, topography, geology, and climate, in turn control the local-scale variables. The characteristics of water bodies are typically governed by the surrounding landscape because aquatic and terrestrial ecosystems are connected by the movement of energy, materials, and organisms across ecosystem boundaries (Polis *et al*., 1997; Soininen *et al*., 2015). For instance, catchment soil and vegetation type influence the amount of allochthonous organic matter and nutrients entering water bodies (Rautio *et al*., 2011; Bartels *et al*., 2012). Owing to such strong connections between aquatic and terrestrial ecosystems, catchment-scale variables may indicate long-term environmental conditions in freshwater ecosystems; therefore, they may be useful in predicting the level of aquatic biodiversity (Soininen and Luoto, 2012; Soininen *et al*., 2015). For example, Soininen and Luoto (2012) recently reported that catchment productivity was associated with the richness of lake planktonic organisms. Microbial communities are also often sensitive indicators of human activities in the catchment, and catchment characteristics may affect microorganisms indirectly through local environmental factors. Human activities can profoundly impair aquatic ecosystems, which is subsequently reflected by microbial communities (Sonneman *et al*., 2001; Walker and Pan, 2006; Jüttner *et al*., 2012). Intensified catchment land use, such as urbanisation, modifies the hydrological cycle, alters water chemistry and changes physical habitat characteristics (Paul and Meyer, 2001). Degradation and homogenisation of freshwater habitats due to anthropogenic activities may also deteriorate habitat heterogeneity and subsequently decrease microbial biodiversity (Passy and Blanchet, 2007).

Although knowledge of microbial biodiversity patterns and determinants has increased during the recent years, considerable knowledge gaps remain especially among small water bodies in northern regions. For instance, even basic taxonomic surveys for spring microogranisms, such as diatoms, are lacking in many regions. Moreover, knowledge of how and why microbial biodiversity varies along elevational gradients in aquatic ecosystems at high latitudes, where species live close to their distributional borders, remains limited. Given that such systems are sensitive to a variety of stressors, including changes in climate and land use (Heino *et al*., 2005; Jyväsjärvi *et al*., 2015; Wang *et al*., 2016), it is essential to increase our understanding of their biodiversity. In high-latitude regions, climatic changes influence, for instance, the length of ice- and snow-free period, habitat availability, water chemistry, and light conditions in aquatic systems, with implications for aquatic biota (Smol *et al*., 2005; Schindler and Smol, 2006; Heino *et al*., 2009; Rühland *et al*., 2013). Microbes are vital for the ecological functions of such systems, underscoring the importance of expanding current understanding of the factors affecting their biodiversity.

1.5 Thesis objectives and scope

The main aim of this thesis is to examine the patterns and drivers of microbial biodiversity across small water bodies in the boreal and subarctic regions. Biodiversity is a complex concept that can be defined and measured using multiple metrics at several spatial scales (Magurran and McGill, 2011). In this thesis, "microbial biodiversity" re-

fers to all measures and indices derived from the biological data. Both taxonomic and functional measures of biodiversity are explored because considering species traits along with taxonomic diversity has recently been recommended to gain deeper insights on the mechanisms structuring communities (Soininen *et al*., 2016; Cadotte and Tucker, 2017). The spatial variation in microbial biodiversity is examined across different types of small water bodies, from pristine subarctic streams and ponds to boreal springs and to human-impacted streams. Although three microbial groups are studied in the subarctic ponds, the emphasis of this work is on the diatoms. A consistent theme throughout this work is to investigate whether microorganisms in small aquatic ecosystems exhibit biodiversity patterns resembling those often observed for macroorganisms. Simultaneously, this thesis aims to identify the relative effects of multi-scale factors, ranging from local environmental factors to catchment-scale, climatic and spatial variables, on aquatic microbial biodiversity in northern regions. Specific objectives are:

O_1 To examine microbial biodiversity patterns and multi-scale drivers along elevational gradients in subarctic streams and ponds (**I** and **II**).

O_2 To identify the effects of species niche characteristics and traits on diatom elevational distributions across subarctic ponds (**III**).

O_3 To test for the theory of island biogeography on diatoms and to identify the factors shaping diatom biodiversity in boreal springs (**IV**).

O_4 To investigate the factors affecting diatom biodiversity along a land-use intensity gradient across boreal streams (paper **V**).

2 Material and methods

2.1 Study areas

The study area in paper **I** was located in northern Finland and Norway (68°58' to 69°23' N, 20°17' to 21°03' E). The study design comprised three subarctic streams and sampling covered sites along an elevational gradient of 21 to 826 m a.s.l. The sampled streams were relatively narrow and had clear waters and turbulent flow.

The study region in paper **II** was also located in northern Finland and Norway (68°55' to 69°58' N, 20°02' to 26°25' E). In this region, 146 subarctic ponds along an elevational gradient of 10 to 1,038 m a.s.l. were sampled. Sampling covered long environmental and climatic gradients, spanning from low-elevation forested landscape to barren boulder fields at high elevations (Figure 3). The sampled ponds were typically small and shallow with clear waters. They were mostly pristine or close to pristine.

The study area in paper **III** was partially the same as in paper **II**, comprising 102 ponds in the Kilpisjärvi–Skibotn region (68°55' to 69°23' N, 20°02' to 21°03' E), sampled along an elevational gradient of 10 to 1,038 m a.s.l. (Figure 4).

The study region in paper **IV** was located in Finland (60°6' to 62°54' N, 23°35' to 30°56' E), spanning hemiboreal, south boreal and middle boreal ecoregions. In total, 50 springs with differing groundwater recharge areas in terms of geology, land cover and land use were sampled.

The study area in paper **V** was located in southern Finland (60°1' to 60°4' N, 24°4' to 25°2' E). In total, 52 streams in this region were sampled. The sampling scheme comprised 52 subcatchments covering a broad land-use intensity gradient from rural to urban landscapes. The catchments of the streams were relatively small (range: 0.2–2.1 km^2) and located at low eleva-

tions (mean elevation range: 3–69 m a.s.l.).

2.2 Field sampling and laboratory methods of local abiotic variables

For paper **I**, the samples were collected in August 2013. Along the course of each stream, sampling sites were located at approximately equal intervals per change in elevation. At each site, diatom samples were collected by brushing the surfaces of 10 randomly selected cobble-sized stones with a toothbrush (25 cm^2 per stone). The sampled stones were measured for length, width, and height. Simultaneously during diatom sampling, conductivity, pH, water temperature (**I**–**V**), total dissolved oxygen concentration, current velocity, stream depth and width were measured, and percentage shading by the riparian canopy was estimated. Water samples were collected for subsequent laboratory analyses (**I**–**V**).

For papers **II** and **III**, the samples were collected in July–August 2015 (For **III** in August). In total, samples from 102 ponds in the Kilpisjärvi–Skibotn region were collected in August and from 44 ponds in Rásttigáisá in July. Along the shoreline of each pond, 10 cobble-sized stones were selected at random from 15–30 cm deep water. By scraping the surfaces of these stones (25 cm^2 per stone) with a sterilised sponge, samples for diatoms (**II** and **III**) and bacteria (**II**) were collected.

Fieldwork for paper **IV** was carried out in 2011 and 2012. In 2011, 37 springs were sampled in May–July. In 2012, 13 springs were sampled in July. In the field, spring width and length were measured, and percentage of shading by the canopy was estimated. To cover all microhabitats in each spring, subsamples from as many different substrata as possible, such as bryophytes, stones, and wood were collected and subsequently pooled into a composite sample for diatoms.

For paper **V**, the samples were collected in

Figure 3. Photographs of the study ponds along the elevational gradient: (a) a wetland pond at 189 m a.s.l.; (b) a mountain birch woodland pond at 627 m a.s.l.; (c) a tundra pond at 795 m a.s.l.; and (d) a boulder field pond at 1,029 m a.s.l. Photo credit: Simon Strömgård.

August 2013. Simultaneously during water sampling, diatoms were sampled by brushing the surfaces of at least six randomly selected cobble-sized stones (25 cm^2 per stone) with a toothbrush.

In the laboratory, water samples were analysed for total nitrogen (TN) following SFS-EN ISO 11905-1 (**I**–**IV**), for total phosphorus (TP) following SFS-EN ISO 6878 (**IV** and **V**) or SFS-EN 1189 (**I**), for Si, Ca, Mg, and K following SFS-EN ISO 11885 (**II** and **III**), and for water colour following SFS-EN ISO 7887 (**IV**). In paper **V**, Ca and Mg were analysed following SFS-EN ISO 14911, NO_3 and SO_4 following SFS-EN ISO 10304-1, and Al, Fe, and Zn following SFS-EN ISO 17294-2. Total suspended solids (TSS) were analysed by first filtering the water samples, then drying the filters in 105°C and finally weighing them (**V**).

2.3 Land cover and land use variables

In paper **II**, normalized difference vegetation index (NDVI) was used as a proxy for terrestrial productivity. The NDVI product was acquired from Landsat 8 Surface Reflectance data (spatial resolution 30 m; United States Geological Survey; Masek *et al*., 2006). The NDVI was computed as a ratio between the near infrared (NIR) and red (R) values: NDVI = (NIR − R) / (NIR + R). Maximal NDVI values were extracted for 30 and 100 m non-overlapping buffer zones surrounding each study site using ArcGIS 10.2.1.

In paper **IV**, the European land cover and

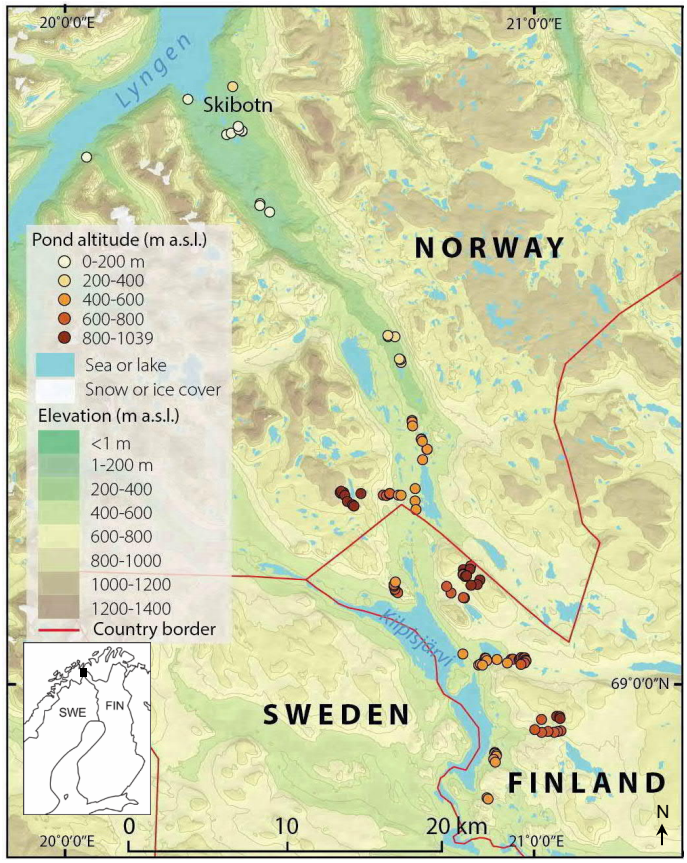

Figure 4. Locations of the 102 study ponds in northern Fennoscandia in paper **III** (National Land Survey of Finland, Topographic Database 09/2015; © Kartverket).

land use classification CORINE Land Cover 2006 database (spatial resolution 25 m; Finnish Environment Institute, 2009) was used as a source of information on land cover and land use surrounding each spring. Using ArcGIS 10.1, the percentage of the area covered by artificial surfaces, agricultural land, forests and seminatural areas, wetlands, and water bodies were calculated. The proportions of different land cover and land use types were extracted for 300 and 1,000 m buffer zones around each spring. To investigate the relationship between diatom species richness and spring isolation, the proportion of the area covered by inland waters within a 3,000 m buffer zone around each spring was also calculated.

In paper **V**, land cover and land use variables were also extracted from the CORINE database (Finnish Environment Institute, 2014). Using ArcGIS 10.1, the stream catchments were first delineated using pipeline data and a digital elevation model (DEM) (National Land Survey of Finland, 2014). Subsequently, the proportion of total catchment area covered by seven different land cover and land use types representing varying levels of anthropogenic activities were calculated. Soil variables, that is, proportion of the total catchment area covered by mineral soil and organic soil, were derived from national soil database (spatial resolution 20 m; Geological Survey of Finland, 2014). DEM was also used to calculate mean slope angle (%) and Kirpich index (Kirpich, 1940), which represents the time of concentration needed for runoff to travel from the most distant point in the catchment to the discharge point. All catchment variables were calculated in ArcGIS 10.1 using zonal statistics tools.

2.4 Climatic variables

In papers **I** and **II**, climatic variables were extracted from WorldClim global climate data, representative of 1950–2000 (spatial resolution c. 1 km^2; Hijmans *et al*., 2005), with ArcGIS 10.2.1. In paper **I**, these data were used to examine whether variation in climatic conditions is greater at higher elevations than at lower elevations. Average monthly minimum and maximum temperature and average monthly precipitation values for the sampling site located at highest and lowest elevation in each stream was extracted. In paper **II**, average July precipitation and average July mean temperature values for each pond were extracted.

2.5 Diatom analysis and metrics

Diatom samples were processed by cleaning them of organic material using wet combustion with hydrogen peroxide (30% H_2O_2) and mounted in Naphrax (**I**–**V**). A total of 300 (**I**, **IV** and **V**) or 500 (**II** and **III**) frustules per sample were counted and identified to the lowest possible taxonomic level (typically to the species level) according to Krammer and Lange-Bertalot (1986, 1988, 1991a,b) and Lange-Bertalot and Metzeltin (1996) using a phase contrast light microscope (Olympus BX40, Melville, NY; magnification 1000×). The local species richness of a site was calculated as the sum of all taxa encountered within the counted frustules (**II** and **V**). In papers **I** and **IV**, extrapolated richness values based on Chao1 (Chao, 1984) richness estimator were used as measures of local species richness.

In paper **III**, the diatom taxa observed in countings were grouped into different life-form and ecological guild categories, and according to cell size. First, the diatom species were classified into five life-form categories described in Rimet and Bouchez (2012): mobile, adnate, stalk-attached, pad-attached, and colonial. Second, the species were assigned to low-profile, high-profile or motile guilds based on their ability to tolerate physical disturbance and use nutrient resources (Passy, 2007a; Rimet and Bouchez, 2012). Furthermore, acid-tolerant and nitrogen-fixing species were separated as distinct guilds

(Van Dam *et al*., 1994; Soininen *et al*., 2016). Third, for each species, minimum and maximum length and width were obtained from the literature (Krammer and Lange-Bertalot, 1986, 1988, 1991a,b; Lange-Bertalot and Metzeltin, 1996). Additionally, the sizes of the 25 species with the highest relative abundances were measured to examine the relationships between the measured sizes and literature-derived values. The measured and literature values correlated positively; the relationship was strongest for minimum width.

2.6 Analysis of bacteria and cyanobacteria

In paper **II**, bacteria were analysed following Wang *et al*. (2017). A phenol–chloroform method was used to extract DNA from biofilm (Zhou *et al*., 1996). Bacterial 16S rRNA genes were amplified in triplicate using primers [515F, 5′-GTGCCAGCMGCCGCGGTAA-3′ and 806R, 5′-GGACTACHVGGGTWTCTAAT-3′]. Agarose gel electrophoresis was used to confirm positive polymerase chain reaction (PCR) products and the PCRs were combined and quantified using PicoGreen (Molecular Probes, Eugene, OR). The PCR products to be sequenced in an Illumina MiSeq run were pooled and purified using a QIAquick Gel Extraction Kit (QIAGEN Sciences, Germantown, MD). The MiSeq Reagent Kit Preparation Guide (Illumina, San Diego, CA) was followed when preparing the sample libraries for sequencing. To assemble overlapped paired-end sequences from Miseq, FLASH was used (Magoč and Salzberg, 2011). The seed-based uclust algorithm was used to cluster the sequences into operational taxonomic unit (OTUs) at 97% pairwise identity (Edgar, 2010). For statistical analyses, the bacteria were rarefied at 8,000 sequences per sample. Cyanobacteria were highly abundant in the bacterial communities and they were separated from the other components of bacteria (hereafter referred to as non-cyanobacteria). For clarity, OTU richness is hereafter referred to as species richness.

2.7 Statistical analyses

The main statistical methods used are presented briefly below (Table 1). Data pretreatment procedures and more detailed descriptions of the statistical analyses are presented in the original papers. All statistical analyses were carried out in R (versions 3.0.2, 3.2.2 and 3.2.4; R Development Core Team, 2016).

The degree of spatial autocorrelation in the local environmental variables and diatom richness was explored using correlograms with Moran's *I* (Moran, 1950) in papers **I** (function *correlog* in the R package pgirmess; Giraudoux, 2014) and **IV** (function *correlog* in the R package ncf; Bjornstad, 2012).

To examine the taxonomic uniqueness of diatom, cyanobacteria, and non-cyanobacteria communities in paper **II**, local contributions to beta diversity (LCBD; Legendre and De Cáceres, 2013) were calculated. By indicating the relative contribution of individual sampling sites to beta diversity, LCBD allows one to identify the sites with above or below average contributions to overall beta diversity. The LCBD values were computed by using Hellinger-transformed abundance data and the function *beta.div* according to the R code by Legendre and De Cáceres (2013).

Generalized linear models (GLMs; McGullagh and Nelder, 1989) were used to identify the key factors explaining variation in the response variables (diatom richness in **I**, **IV** and **V**; diatom, cyanobacteria, and non-cyanobacteria richness and LCBD in **II**). The best approximating model was selected, using Akaike's information criterion (AIC; Akaike, 1974) and the function *stepAIC* in the R package MASS with backward stepwise model selection (Venables and Ripley, 2002) (**I**, **II**, **IV**, **V**). In paper **III**, GLMs were used to investigate the occurrence

Table 1. Overview of the study systems and microbial groups, response and explanatory variables, and main statistical methods used in papers **I**–**V**. ANOSIM = Analysis of similarities; BRT = Boosted regression trees; FDis = Functional dispersion index; GLM = Generalized linear model; HP = Hierarchical partitioning; LCBD = Local contribution to beta diversity; LM = Linear regression model; NDVI = Normalized difference vegetation index; OMI = Outlying mean index; RDA = Redundancy analysis; SEM = Structural equation model; VP = Variation partitioning.

Paper	Ecosystem (study sites)	Microbial group(s)	Response variables	Explanatory variables	Main statistical methods
I	Subarctic streams (44)	Diatoms	Local species richness, beta diversity, elevational range size	Local chemical and physical variables, site elevation	ANOSIM, BRT, GLM, HP, LM, Mantel and partial Mantel tests, Mid-point method, Moran's *I*
II	Subarctic ponds (146)	Diatoms, cyanobacteria, non-cyanobacteria	Local species richness, LCBD	Local chemical variables, NDVI, climatic variables, pond elevation	GLM, LCBD, LM, SEM, VP
III	Subarctic ponds (102)	Diatoms	Elevational range size, occurrence, trait diversity	Local chemical variables, pond elevation, niche characteristics, traits	FDis, GLM, LM, OMI
IV	Boreal springs (50)	Diatoms	Local species richness, beta diversity	Local chemical and physical variables, catchment land cover and land use, spring isolation and location	ANOSIM, GLM, LM, Mantel and partial Mantel tests, Moran's *I*
V	Boreal streams (52)	Diatoms	Local species richness, community composition	Local chemical and physical variables, catchment land cover and land use, soil type, topography, and Kirpich index	ANOSIM, GLM, LM, RDA, VP

and elevational range size of diatoms in relation to the life-forms and ecological guilds (categorical variables), and minimum cell width (continuous variable).

Linear regression was used to investigate the relationship between diatom species richness and spring area (length × width) and isolation (**IV**), and between diatom species richness and local environmental and catchment variables (**V**). Linear regression was also used to examine richness–elevation, LCBD–elevation, and richness–LCBD relationships in paper **II**. To identify a possible nonlinear elevational pattern, models with a quadratic term of elevation were also constructed.

In paper **I**, the independent effect of each explanatory variable on diatom richness was analysed using hierarchical partitioning (Chevan and Sutherland, 1991). Hierarchical partitioning was ran using function *hier.part* in the R package hier.part (Walsh and Mac Nally, 2013). The effects of the explanatory variables on diatom richness were also explored using a boosted regression tree (BRT) method (Elith *et al*., 2008) in paper **I**. The BRTs were fitted using function *gbm* in the R package gbm (Ridgeway, 2013).

In paper **II**, structural equation models (SEMs; Grace, 2006) were constructed to examine the causal relationships between the hierarchical explanatory variables (i.e., local variables, NDVI, and elevation) and richness or LCBD of the three microbial groups (i.e., diatoms, cyano-

bacteria, and non-cyanobacteria). Both direct and indirect pathways were considered in the models. A chi-square test was used to evaluate the model's goodness of fit; a non-significant *P*-value (> 0.05) denotes that the model is consistent with the data (Grace and Bollen, 2005). The SEMs were fitted using function *sem* in the R package lavaan (Rosseel, 2012).

Variation partitioning (Borcard *et al*., 1992) was used to study the pure and joint effects of local variables, NDVI, and elevation on species richness and LCBD of diatoms, cyanobacteria and non-cyanobacteria in paper **II**, and the pure and joint effects of local factors and catchment variables on diatom species richness and community composition in paper **V**. Variation partitioning was conducted using the function *varpart* in the R package vegan (Oksanen *et al*., 2013).

To investigate change in diatom community composition along environmental and spatial gradients in papers **I** and **IV**, Mantel test was used (Mantel, 1967; Legendre and Legendre, 2012). Similarity matrices (similarity = 1 − dissimilarity) were first created for the diatom data. To calculate the pairwise similarities, the Bray–Curtis similarity index was used on diatom relative abundance data (**I** and **IV**), and the Jaccard similarity index on diatom presence–absence data (**I**). By calculating pairwise Euclidean distances, distance matrices were constructed separately for the local environmental data and geographical data (i.e., elevation in **I**; spring coordinates in **IV**). Furthermore, partial Mantel tests were carried out to disentangle the pure effects of local environmental and geographical variables on diatom community similarity (**I** and **IV**). The statistical significances of the relationships were assessed using 9999 permutations. Mantel and partial Mantel tests were conducted using functions *mantel* and *mantel.partial* in the R package vegan (Oksanen *et al*., 2013).

To examine diatom beta diversity in paper **I**, initial compositional similarities and halving distances of the distance decay relationships were calculated (Soininen *et al*., 2007). The initial similarity (at 1 m distance) was calculated following the equation $Sim_1 = \beta \times 1 + \alpha$, and halving distance following the equation $HD = (\beta - \alpha) / 2\beta$, where β and α are regression parameters.

In paper **V**, redundancy analysis (RDA) was conducted to explore variation in diatom community composition in relation to the local factors and catchment variables. RDA was carried out using function *rda* in the R package vegan (Oksanen *et al*., 2013).

Analysis of similarities (ANOSIM; Clarke, 1993) was used to test whether there were significant differences in diatom species compositions between the streams in paper **I**, between the springs located in different ecoregions in paper **IV**, and between the streams belonging to different land-use intensity groups in paper **V**. In paper **V**, also differences in stream water quality between the land-use intensity groups were tested.

A mid-point method (Rohde *et al*., 1993) was used to test whether diatom distributions agree with the Rapoport's elevational rule (**I**). The elevational range size of diatoms was computed as the difference between each species minimum and maximum elevation of occurrence (**I**). The mid-point of elevational range was calculated as the mean between each species minimum and maximum elevation of occurrence.

Species distributions in paper **III** were defined using two metrics: occurrence and elevational range size. Occurrence referred to the number of ponds in which a species was observed. Elevational range size was calculated as the difference between each species minimum and maximum elevation of occurrence. For species observed in one pond only, the elevational range size was set to 2 m. To circumvent dependence (i.e., circularity) between the metrics of species distributions and niche characteristics,

independent diatom and water chemistry data were used to examine their relationships (**III**). The diatom species niche characteristics (niche position and niche breadth) were, therefore, derived from a surface-sediment diatom data set comprising 141 northern Fennoscandian lakes (Korhola *et al*., 1999; Weckström and Korhola, 2001; Weckström *et al*., 2003). The niche position and niche breadth were obtained by outlying mean index (OMI) analysis (Dolédec *et al*., 2000). The calculation of niche values was carried out by using Hellinger-transformed relative abundance data, the key environmental variables and the function *niche* in the R package ade4 (Dray and Dufour, 2007). To examine trait diversity at the community level in paper **III**, a functional dispersion index (FDis; Laliberté and Legendre, 2010) was utilised. The functional dispersion was calculated by using the function *dbFD* in the R package FD (Laliberté and Legendre, 2010; Laliberté *et al*., 2014).

Finally, linear regression was used to investigate the relationship between the breadth and mid-point of elevational range of diatom species (**I**); between diatom species occurrence or elevational range size and niche position or niche breadth (**III**); and between diatom functional diversity (FDis) and explanatory variables (i.e., elevation and local environmental factors) (**III**).

3 Results and discussion

3.1 Multi-scale drivers of elevational microbial biodiversity (Papers I and II)

Paper **I** investigated the patterns and drivers of diatom species richness and beta diversity along elevational gradients in subarctic streams. The key environmental factors affecting species richness were identified, the validity of the Rapoport's elevational rule was tested, and the relative effects of local environmental variables and elevation in shaping diatom beta diversity were determined. Within the individual study streams, no significant relationships between richness and elevation existed (**I**). This finding contradicts with those of Wang *et al*. (2011) and Ormerod *et al*. (1994), who reported declining trends in diatom richness with increasing elevation in a Chinese and a Nepalese stream system, respectively. In contrast, in a study by Wang *et al*. (2017), diatoms richness showed mostly no elevational trends in European and Asian streams. Similarly, Jüttner *et al*. (2010) reported that diatom richness and diversity did not correlate with elevation in Himalayan streams. These findings suggest that rather than being controlled only by elevation and associated climatic gradients, stream diatom richness may respond more directly to local-scale variables, such as pH (Wang *et al*., 2017) or the frequency of disturbances (Jüttner *et al*., 2010).

Water depth was identified by GLM, hierarchical partitioning and BRT as the most important factor explaining the variation in diatom richness, with additional effects by substrate size, water chemistry, and elevation (**I**) (Figure 5a). Richness increased with water depth. Water depth typically indicates light availability at the stream bottom, thus being an important variable for benthic primary producers (Virtanen and Soininen, 2012). In the clear-watered systems studied here, the occurrence of diatoms is unlikely to be limited by light availability. The effect of water depth on diatom richness is speculative at present, but it may be linked to disturbance frequency and intensity associated with flow fluctuations. The effect of natural physical disturbances in driving species diversity is widely recognised (Connell, 1978; Sousa, 1979), and spatial and temporal flow variations are known to influence stream diversity, structure and function (Peterson and

Stevenson, 1992; Townsend *et al*., 1997; Biggs *et al*., 2005). Deeper stream sections are less vulnerable to water level fluctuations, such as desiccation and flood disturbance, consequently being able to maintain higher diatom richness. A low diatom richness may hence be attributable to high level of disturbance at shallow stream sites, leading to species-poor communities comprising species capable of colonising or persisting under such circumstances (Biggs and Smith, 2002; Soininen and Heino, 2007).

Stream diatoms did not follow the Rapoport's elevational rule because species elevational ranges did not widen consistently with increasing elevation, implying that diatom distributions were shaped more strongly by other than climatic variables (**I**). This outcome concurs with Wang and Soininen (2017) and Fu *et al*. (2004), who found no evidence for the Rapoport's elevational rule for stream bacteria, diatoms, or macroinvertebrates in Asia and Europe, or for freshwater fishes in China, respectively. In contrast, a positive relationship between range size and elevation was reported for insects along a stream elevational gradient in Russia (Beketov, 2009). Such contrasting findings suggest that the relationship between range size and elevation is context-dependent; contingent on the specific characteristics of the study region and species. Although the climatic data used in this study indicated that climatic conditions varied more at high elevations compared to low elevations, the climatic gradients were probably relatively short to strongly affect range sizes, especially regarding the physiological tolerances of diatoms. Further studies using a wide range of taxa and ecosystems differing in biotic and abiotic characteristics would be useful for elucidating el-

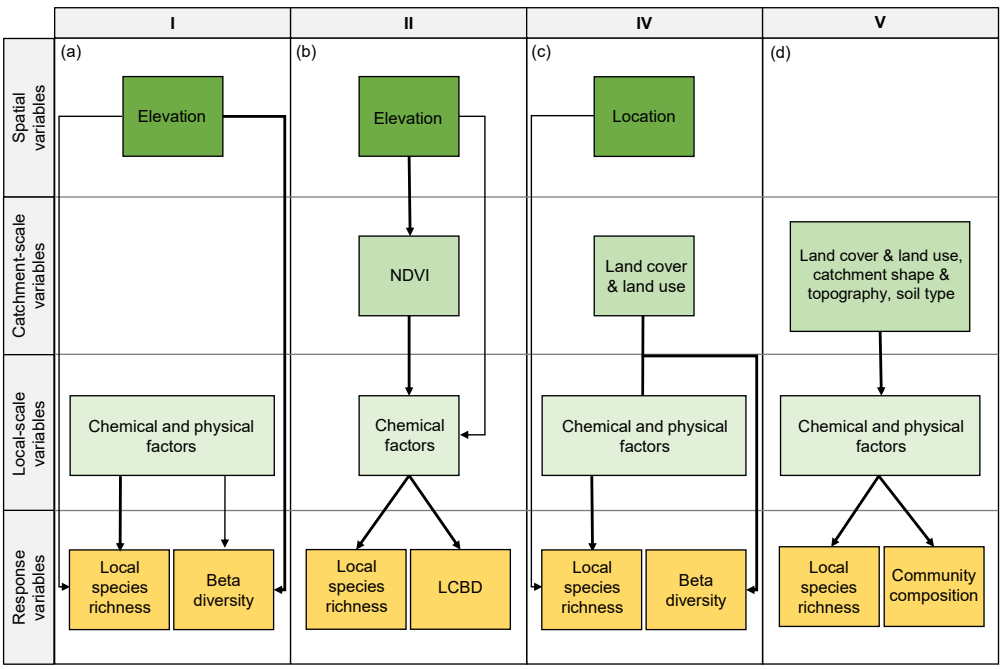

Figure 5. Multi-scale factors associated with diatom biodiversity in papers (a) **I**, (b) **II**, (c) **IV** and (d) **V**. Paper **III** was not considered here as no hierarchical drivers were identified in that paper. The models portray the associations between explanatory variables at different spatial scales and diatom biodiversity metrics. Width of arrows indicate relative importance of the explanatory variables. NDVI = normalized difference vegetation index; LCBD = Local contribution to beta diversity.

evational patterns in range size and underlying mechanisms (Wang and Soininen, 2017).

Mantel and partial Mantel tests illustrated that in each study stream, community similarity decreased significantly with elevational distance, while the distance decay with environmental distance was weaker and typically non-significant (**I**) (Figure 5a, Figure 6a). The observed distance decay with elevation is congruent with the notion that freshwater diatom communities often exhibit spatially structured variation (Soininen *et al*., 2004; Heino *et al*., 2010; Smucker and Vis, 2011; Wang *et al*., 2012; Jyrkänkallio-Mikkola *et al*., 2017), and could stem from dispersal-related factors, so that species compositions between neighbouring sites tend to be more similar than between sites farther apart. However, considering that the sites within the streams were probably linked by unidirectional dispersal, and that the effects of spatial factors on aquatic microbial communities are often stronger at larger spatial scales (Verleyen *et al*., 2009; Soininen *et al*., 2011; Tang *et al*., 2013), also other than factors related to dispersal presumably affected the changes in community compositions. For instance, some unmeasured, spatially structured abiotic or biotic variables may have influenced diatom community composition and distance decay along the stream elevational gradients.

Diatom richness and community composition responded differently to the elevational gradients (**I**). Such decoupling of the two metrics highlights the advantage of considering multiple aspects of biodiversity when examining the driv-

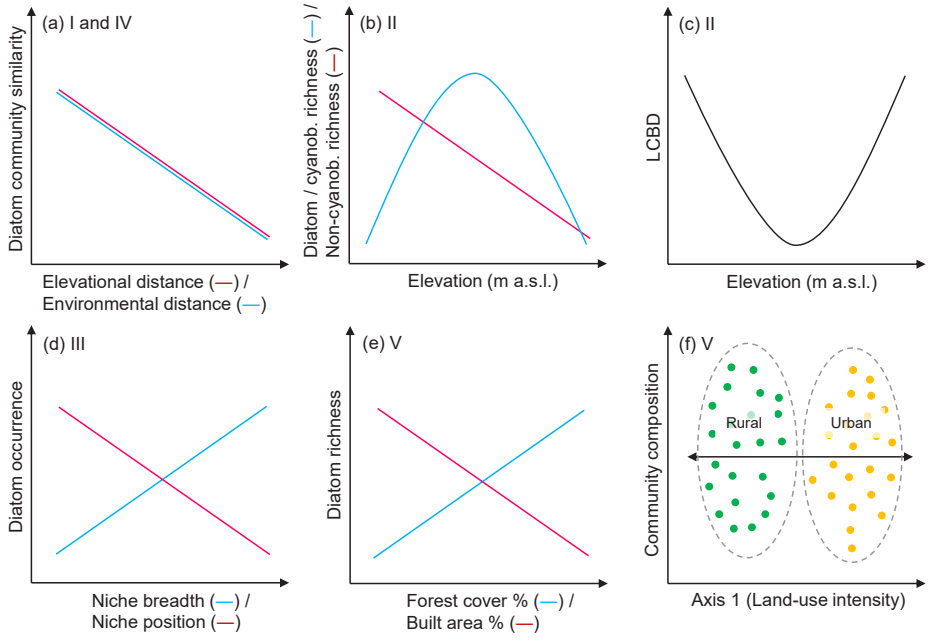

Figure 6. Representation of the observed microbial biodiversity patterns in papers **I**–**V**. The plots illustrate the directions of the trends, not their strength. (a) Diatom community similarity decreased with elevational distance in the subarctic streams (**I**); Diatom community similarity decreased with environmental distance in the boreal springs (**IV**). (b) Diatom and cyanobacteria richness exhibited unimodal elevational trends, whereas non-cyanobacteria richness declined with elevation in the subarctic ponds (**II**). (c) The relationship between LCBD (local contribution to beta diversity) and elevation was U-shaped for all studied microbial groups (i.e., diatoms, cyanobacteria, and non-cyanobacteria) in the subarctic ponds (**II**). (d) There was a positive relationship between diatom occurrence and niche breadth, and a negative relationship between diatom occurrence and niche position in the subarctic ponds (**III**). (e) Diatom species richness increased with catchment forest cover and decreased with the proportion of built areas in the boreal streams (**V**). (f) Diatom community composition changed along the land-use intensity gradient in the boreal streams (**V**).

ing factors. Investigating not only species richness, but also changes in community composition provides deeper insights into the responses of biological communities to changing environmental conditions. Nevertheless, the local species richness can provide valuable information regarding the level of stress and disturbance prevailing at a site. Impoverished diatom communities may denote high level of physical disturbances (**I**) or chemical stress (**II**).

The results further showed that initial compositional similarities and elevational halving distances differed among the streams, and the results of ANOSIM revealed that the three streams harboured significantly different community compositions (**I**). These findings imply that multiple factors contributing to stream characteristics, such as topography, stream connectivity, and water chemistry create distinct diatom communities even across such pristine systems within a relatively small geographical extent. Moreover, the results lend support for the fact that among-site connectivity and flow directionality are important for passively dispersing organisms in lotic ecosystems (Liu *et al*., 2013).

Paper **II** focused on examining the microbial biodiversity patterns along an elevational gradient across subarctic ponds. The elevational trends in species richness and LCBD of diatoms, cyanobacteria, and non-cyanobacteria were investigated, and, using SEMs, the direct and indirect effects of multi-scale factors on richness and LCBD were identified. LCBD was used to measure the uniqueness of individual sampling sites in terms of community composition; high values denote sites with unique community compositions in the data. All the studied microbial groups showed clear elevational richness and LCBD patterns (**II**). The SEMs revealed that microbial richness and LCBD were affected by hierarchically structured, causally-related factors (Figure 5b). Elevation controlled NDVI and influenced pond variables, such as TN, both directly and indirectly via NDVI.

The results were highly similar for diatoms and cyanobacteria, with unimodal elevational patterns for richness (Figure 6b) and U-shaped for LCBD (Figure 6c) (**II**). Such congruence implies similar driving mechanisms for the biodiversity of these two groups of aquatic primary producers. The unimodal relationship between richness and elevation is common among macroorganisms (Rahbek, 2005) and occasionally also observed for aquatic microbes (Weckström and Korhola, 2001; Wang *et al*., 2017). For LCBD, the U-shaped elevational pattern implies that ponds at both ends of the elevational gradient may harbour communities with more specialist species (Legendre and De Caceres, 2013). Based on SEMs and variation partitioning, local pond variables were the most important factors contributing to the variation in diatom and cyanobacteria richness and LCBD (**II**), complementing evidence emphasising the importance of environmental factors for aquatic autotrophs (Verleyen *et al*., 2009; Stomp *et al*., 2011; Wang *et al*., 2017). In the final SEMs, pH exerted the strongest direct effect on richness and LCBD of both groups; species richness increased with pH and LCBD decreased with pH. Thus, low pH may act as an abiotic filter excluding species intolerant of acidic conditions, resulting in impoverished, yet taxonomically unique communities dominated by a few acid-tolerant species. This result agrees with earlier studies on the importance of pH for aquatic primary producers (Weckström *et al*., 1997; Bennett *et al*., 2010; Soininen *et al*., 2016; Wang *et al*., 2017).

In contrast to the unimodal richness-elevation patterns of diatoms and cyanobacteria, non-cyanobacteria richness declined with elevation (**II**) (Figure 6b). Based on a recent meta-analysis, such a pattern is occasionally found for freshwater and soil bacteria, but other than decreas-

ing trends are also often observed; hence, elevational richness patterns for bacteria remain elusive (Wang *et al*., 2017). Non-cyanobacteria LCBD showed U-shaped elevational patterns similarly as diatom and cyanobacteria LCBD (Figure 6c). In SEM, elevation had the strongest direct (negative) effect on non-cyanobacteria richness and LCBD (**II**). Elevation affected non-cyanobacteria also indirectly via catchment productivity and water chemistry. These findings suggest that climatic factors are highly important in driving bacterial biodiversity, and that the relative importance of the hierarchical determinants differ between the heterotrophs and autotrophs. The autotrophs were most strongly controlled by local pond variables, whereas the heterotrophs were also influenced by elevation and terrestrial productivity. Given that every investigated component of microbial biodiversity was directly or indirectly associated with elevation, climatic changes are likely to alter aquatic microbial assemblages in northern regions. Predicting precisely how communities may change in response to climatic changes using these data is uncertain, however, because the elevational patterns in richness and LCBD were mostly nonlinear, there were complex interactions among the explanatory variables, and the ponds were sampled only once.

Interestingly, there were contrasting richness–LCBD relationships among the taxonomic groups (**II**). There was a negative correlation between the two metrics for diatoms and cyanobacteria, complying with recent observations for stream diatoms (Pajunen *et al*., 2017; Vilmi *et al*., 2017), freshwater fish (Legendre and De Cáceres, 2013) and urban pond insects (Heino *et al*., 2017a). These findings denote that sites with low species richness tend to have more unique species compositions; therefore, species richness alone is insufficient to identify taxonomically unique communities. The negative LCBD–richness relationship is, though, clearly not a universal rule across multiple taxa because there was a positive correlation between the two metrics for non-cyanobacteria (**II**). From a conservation point of view, preserving not only species-rich ponds, but also taxonomically unique, species-poor ponds may be a prerequisite for conserving aquatic biodiversity in the subarctic.

3.2 Niche characteristics and traits in shaping elevational diatom distributions (Paper III)

Paper **III** explored the effects of species niche characteristics and traits on diatom distributions, and identified the factors associated with trait diversity along elevational gradients across subarctic ponds. The results illustrated that diatom occurrence was positively correlated with niche breadth, implying generalists had wider distributions than specialists, and negatively with niche position, suggesting non-marginal species were more widely distributed than marginal species (**III**) (Figure 6d). These findings generally lend support for the importance of niche characteristics for species distributions reported among both micro- (Heino and Soininen, 2006; Passy, 2012; Wang and Soininen, 2017; Rocha *et al*., 2018) and macroorganisms (Heino and Grönroos, 2014; Wang and Soininen, 2017; Rocha *et al*., 2018).

Overall, however, the results emphasised the primacy of a single environmental variable, that is, pH as a key factor affecting diatom distributions (**III**). First, a high tolerance towards pH was associated with a wider occurrence and elevational range size. Second, the GLMs showed that acid-tolerant species were more widely distributed than species intolerant of acidic conditions. The reason why acid tolerance seems such a beneficial trait among benthic diatoms probably stems from the limnological characteristics

of the ponds in this subarctic region. Nearly half of the study ponds were acidic and the lowest pH values were typically measured either at low or high elevation ponds. Consequently, to attain a broad elevational distribution, a species must be capable of tolerating acidic conditions. The species with widest distributions across the study ponds, that is, *Brachysira brebissonii, Frustulia saxonica*, *Psammothidium marginulatum* and *Tabellaria flocculosa*, are indeed categorised in the literature as acidophilous or acidobiontic (Van Dam *et al*., 1994). The frequent occurrences of these acid-tolerant species imply that specialisation towards acidity does not prevent a wide distribution, contrasting the expectation that exclusively generalists should have widest distributions (Bennett *et al*., 2010).

Along with acid tolerance, another trait significantly associated with diatom distribution was cell size (**III**). Cell size was negatively correlated with both occurrence and elevational range size, thereby concurring with what was expected for small and passively dispersing organisms (Heino and Soininen, 2006; Passy, 2012; Rocha *et al*., 2018). The negative trend between microbial cell size and regional distribution implies that smaller species have a more efficient dispersal ability, promoting a wider regional distribution compared with larger-sized species (Heino and Soininen, 2006; Passy, 2007b, 2012).

At the community level, trait diversity measured as functional dispersion correlated positively with pH and negatively with conductivity (**III**). In contrast to a priori hypothesis (Wang e*t al*., 2012; Bässler *et al*., 2016) and a recently reported pattern for larger organisms (Bässler *et al*., 2016), trait diversity of diatoms did not decrease with elevation. It was expected that harsh environmental conditions prevailing at high elevations results in low trait diversity, that is, communities composed of species that are functionally similar and competitively superior compared to other species. Contrary to this hypothesis, the results showed that rather than elevation and the associated climatic factors, local abiotic variables may be more essential in shaping diatom trait diversity in subarctic ponds. Although a relatively small fraction of the variation in trait diversity was captured by these explanatory variables, the results did illustrate that several acidic wetland ponds at low elevations harboured particularly low trait diversity. This outcome is in line with the taxonomically species-poor communities found in acidic conditions along the same pond elevational gradient (**II**). Low pH seems to operate as an abiotic filter selecting for acid-tolerant species, and resulting in impoverished, functionally clustered communities.

3.3 Factors affecting spring diatom biodiversity (Paper IV)

Paper **IV** presented the first insights into spring diatom communities in Finland. The main predictions of the theory of island biogeography were tested, and the roles of local environmental and geographical factors in shaping diatom richness and community composition were determined. Diatom richness did not conform to the main predictions of the theory of island biogeography; neither spring area nor isolation significantly explained the variation in richness (**IV**). For benthic diatoms, SARs have rarely been studied, but in a recent study, Bolgovics *et al*. (2016) reported that among lentic water bodies, diatom richness increased with area. The results also contradict with those of Smith *et al*. (2005) and Stomp *et al*. (2011), who reported positive SARs for phytoplankton, but agree with Soininen and Luoto (2012), reporting a lack of SAR for phytoplankton in boreal lakes.

Several reasons for the lack of SAR for spring diatom richness can be proposed. First, environmental heterogeneity typically increases with ar-

ea. This increase in environmental heterogeneity with area coupled with species specificity for different habitats has been invoked to underlie a positive SAR also for microbes (Horner-Devine *et al*., 2004). In these data, however, larger spring area did not necessarily translate into higher habitat heterogeneity, as springs are inherently complex, and several factors, such as water depth, microhabitat complexity, and riparian shading, influence spring heterogeneity independently of its size (Cantonati *et al*., 2012a). Second, area is assumed to affect the rate of local extinctions. Larger islands should support larger populations, which are less susceptible to local extinctions (MacArthur and Wilson, 1967). As several small springs also exhibited relatively high species richness, it seems that diatom richness in springs was not constrained by extinctions. It can be that the rates of local extinctions are reduced via rescue effects owing to permanent algal seed banks in the springs (Smith *et al*., 2005). Third, this study was not conducted on a nested study design in which a larger area contains smaller ones but based on individual springs with varying environmental conditions. While this variability enables the identification of species sorting along environmental gradients, it may have hampered the detection of relationships between richness and spring area and isolation. The lack of richness–isolation relationship also implies that isolation does not apparently limit immigration and suggests effective dispersal among this group of passively dispersing microorganisms. At the relatively small spatial scales considered here, site connectivity thus seems to be of minor importance for diatoms. At larger regional and global scales, isolation, habitat connectivity and dispersal limitation may be more essential for freshwater diatom diversity (Vyverman *et al*., 2007; Benito *et al*., 2018).

The primacy of environmental factors in explaining diatom biodiversity was emphasised throughout the study. Based on GLMs, the variation in diatom richness was affected mostly by local factors, that is, nutrients, pH, conductivity, water colour and temperature, and shading (**IV**) (Figure 5c). Richness was also associated with latitude, the effect of which possibly indicated spatial variation in the measured environmental variables. A high number of species was typically recorded in springs where the prevailing environmental conditions were average in terms of multiple explanatory variables. In contrast, impoverished communities appeared under harsh growing conditions regarding one or more of the explanatory factors. This outcome concurs with Soininen and Heino (2007), who showed that among boreal stream diatoms, highly diverse communities occurred at sites where species occurrences were not limited by local resource or stress factors. Mantel and partial Mantel tests demonstrated that the community similarity significantly correlated with environmental distance (Figure 5c, Figure 6a), whereas no correlation between community similarity and geographical distance was observed (**IV**), indicating that the effects of environmental factors override those of spatial ones on the spring diatom communities. Local-scale variables, such as conductivity, pH, nutrient concentrations (Cantonati, 1998; Cantonati and Spitale, 2009; Gesierich and Kofler, 2010; Cantonati *et al*., 2012b; Mogna *et al*., 2015), and shading (Cantonati and Spitale, 2009; Cantonati *et al*., 2012b) are often reported to have an effect on spring diatom communities in other regions, such as the Alps, and the results of this study also highlight their primary role in structuring communities.

The weak spatial structuring of communities was further emphasised in ANOSIM results, showing no significant differences in community compositions between the ecoregions (**IV**). At the spatial scale of this study (< 500 km), diatom communities seem to be strongly controlled by

environmental factors but unaffected by dispersal limitation. The relative importance of environmental and spatial factors on freshwater diatom communities is often scale-dependent, and dispersal limitation is likely to act more strongly at larger spatial scales (Soininen, 2007; Verleyen *et al*., 2009).

3.4 Diatom biodiversity along a land-use intensity gradient (Paper V)

Paper **V** investigated the effects of local environmental and catchment variables on stream diatom richness and community composition along a land-use intensity gradient in an urbanised, boreal region. The study revealed that the number of species increased with increasing catchment forest cover and decreased with increasing proportion of built areas (Figure 6e). While in forested streams the mean number of species was 43, the corresponding figure in urban streams was 21. In addition to declining species richness, diatom community composition also changed along the rural–urban gradient (Figure 6f), and more intensive land use resulted in the occurrence of pollution-tolerant species. Based on ANOSIM, also community composition differed between the streams in different land-use intensity groups (**V**).

The clear segregation of diatom communities following land use patterns indicates that catchment-scale variables integrate water chemistry temporally and mirror longer-term environmental conditions compared with snapshot water sampling. Exploring the factors underlying the observed patterns indeed underscored the joint effects of local and catchment characteristics on diatom communities. Species richness and community composition were associated with local variables, including water temperature, nutrients, conductivity, and aluminium concentration, which in turn reflected catchment properties, such as land cover and land use (**V**) (Figure 5d). In variation partitioning, the variation in community composition and species richness was best explained by the combined effects of local stream variables and catchment characteristics, while their individual effects were notably weaker. This finding suggests connections between the variables in these groups, and that catchment characteristics are key determinants of water quality (Allan, 2004; Varanka and Luoto, 2012; Taka *et al*., 2016) and consequently of stream microbial communities (Jyrkänkallio-Mikkola *et al*., 2017).

The results illustrated how anthropogenic activities and associated physicochemical changes can have profound consequences for aquatic microbial biodiversity; hence, they are vital indicators of the cumulative effects of such stressors (Walker and Pan, 2006). Owing to the effects of urbanisation, declines in diatom diversity and substantial changes in community composition, often with a shift towards more pollution-tolerant species composition, have been observed in many regions globally (Sonneman *et al*., 2001; Jüttner *et al*., 2003, 2012; Newall and Walsh, 2005; Ndiritu *et al*., 2006; Walker and Pan, 2006; Chen *et al*., 2016). Similarly, urbanisation has profoundly affected biodiversity across trophic levels and ecosystems, often promoting the loss of diversity (Riley *et al*., 2005; McKinney, 2008; Aronson *et al*., 2014).

3.5 Methodological issues

Inevitably, some methodological issues possibly influencing the results stem from the fact that the biodiversity metrics and indices are derived from sample-based data. There is uncertainty regarding the relationship between measured and true microbial biodiversity. For instance, elevational range sizes may have been underestimated for some rare, undetected species. Also, although the

seemingly restricted distributions of large diatom species compared with small-sized species can be explained by species characteristics, it may also be attributable to the typically lower abundances of large species in the samples compared with small species. Uncertainty in the measured diatom diversity may also be due to the morphological species identification, the taxonomic resolution used, and because diatom species can exhibit cryptic diversity and phenotypic plasticity (Vanormelingen *et al*., 2008). Comparing results obtained using traditional morphological methods and molecular techniques is likely to provide new insights into the diversity and distributions of diatoms (Zimmermann *et al*., 2015; Vasselon *et al*., 2017; Rivera *et al*., 2018).

Several explanatory variables were found to contribute to the spatial variation in microbial communities, yet a large amount of variation remained unexplained in some occasions, indicating that microbial biodiversity is shaped by a variety of interacting factors at multiple scales. The high proportion of unexplained variation may be due to the effects of some unmeasured factors, such as biotic interactions (Liess *et al*., 2009; Jyrkänkallio-Mikkola *et al*., 2016) or physical disturbances. Alternatively, the used snapshot sampling may not precisely represent the actual, spatiotemporally varying environmental conditions faced by the microbial communities. The large amount of unexplained variation may also in part be attributable to stochasticity in the occurrences of microbial species (Soininen *et al*., 2013).

Yet another methodological issue concerns using spatial variables as proxies for dispersal as they may not precisely reflect actual dispersal rates. For example, the methods used to measure spring isolation may partially explain the outcome of no relationship between diatom richness and spring isolation. Measuring local environmental factors is more straightforward than measuring actual dispersal events and rates in natural communities (Lindström and Langenheder, 2012; Heino *et al*., 2017b); hence, there is uncertainty as to whether the used spatial variables accurately represented spring isolation and potential dispersal limitation.

4 Conclusions and future perspectives

This thesis provided new insights into the patterns and multi-scale drivers of microbial biodiversity across small water bodies in northern regions. Small water bodies are essential components of biodiversity in northern landscapes; yet, the biota they support, especially at the microbial level, has remained understudied. This study showed that the patterns in and factors affecting microbial biodiversity vary among the streams, ponds, and springs, and focal taxonomic groups. Microbial biodiversity in small water bodies is influenced by a variety of factors operating at hierarchical spatial scales, the relative importance of which is context-dependent. The effects of local environmental variables were emphasised throughout, yet catchment properties and spatial factors may also be essential.

Along stream elevational gradients, there were no consistent trends in diatom species richness or range sizes, whereas changes in community compositions were mainly associated with elevational distance. Diatom communities in such systems seem to be shaped by interacting local-scale variables, such as water depth, and regional drivers, including dispersal and geographical factors. Along pond elevational gradients, diatoms and cyanobacteria showed unimodal richness–elevation patterns, whereas non-cyanobacteria exhibited a decreasing trend. Low- and high-elevation ponds harboured taxo-

nomically unique microbial communities, suggesting that both ends of the elevational gradient may harbour aquatic communities with relatively high proportion of specialist species. The effects of multi-scale factors in driving the observed patterns were apparent in the SEMs, which illustrated that climate-induced changes in terrestrial vegetation and local-scale variables result in changing aquatic microbial communities along elevational gradients. The relative importance of the hierarchical explanatory variables differed between the autotrophs and heterotrophs, highlighting the importance of considering multiple taxonomic groups with differing functional roles for a deeper understanding of biodiversity patterns and processes. Moreover, not treating all bacteria as a single unit is encouraged, as differentiating cyanobacteria from the other components of bacteria revealed distinct patterns for the two groups. To increase current understanding of elevational microbial biodiversity, temporal aspects could be examined in the future. Little is known about temporal variation in aquatic microbial diversity and community composition along elevational gradients and studies determining such variability would shed light on how and why microbial biodiversity varies not only in space, but also through time.

Diatom distributions across the subarctic ponds were shaped by species niche characteristics and traits. The key traits associated with species distributions were tolerance towards acidity and cell size: acid tolerance and small size were associated with a broader elevational distribution. The effect of pH in constraining diatom biodiversity was further emphasised at the community level; functionally clustered communities occurred in acidic ponds, reflecting stressful environmental conditions that favour acid-tolerant species. Regarding species traits, intraspecific differences in diatom body size along elevational gradients could be investigated in the future.

In springs, diatom species richness and community composition were controlled by local-scale variables and land cover and land use, whereas no evidence for species–area or species–isolation relationships emerged. At the relatively small spatial scales covered here, dispersal-related factors do not seem to constrain diatom biodiversity. Thus, local spring diatom communities are structured primarily by environmental factors. Research on spring diatom biodiversity in northern regions is still in its infancy and more studies are needed to assess the relative importance of environmental and spatial factors in structuring communities at larger spatial scales.

Along the land-use intensity gradient, stream diatom richness declined and community composition shifted towards more pollution-tolerant species. These patterns were most strongly driven by the joint effects of local-scale and catchment variables, emphasising the intertwined relationship between the hierarchical factors affecting microbial communities.

Looking ahead, a future research plan is to examine microbial biodiversity in aquatic ecosystems even smaller than in this thesis using both observational and experimental methods. Both natural ecosystems and experimental microcosms are investigated because accompanying observational studies with experimental ones promote the identification of causal factors affecting communities. The primary aim of this study is to determine the factors controlling microbial communities in natural rock pools and experimental aquatic microcosms along marine–freshwater transitions on the Baltic Sea islands. The Baltic Sea archipelago comprises numerous islands of varying size and distance to the mainland, and numerous rock pools within islands, providing an ideal setting for studies in the framework of island biogeography and metacommunity theory. Using aquatic microcosms (Wang e*t al*., 2016), the aim is to carry out dispersal ex-

periments and to investigate the effects of environmental stress on microbial biodiversity.

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